THE KANSAS UNIVERSITY SCIENCE BULLETIN.

Vol. V, No. 7—October, 1909.
(Whole Series, Vol. XV, No. 7.)

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KOEBERLINIA SPINOSA ZUCC.: AN ECOLOGICAL STUDY OF THE ANATOMY OF THE STEM AND SOME OTHER PARTS, ... *Miriam Sheldon.*

PUBLISHED BY THE UNIVERSITY,

LAWRENCE, KAN.

Entered at the post-office in Lawrence as second-class matter.

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VOL. V, NO. 7] OCTOBER, 1909. [WHOLE SERIES VOL. XV, NO. 7

KOEBERLINIA SPINOSA ZUCC.:

AN ECOLOGICAL STUDY OF THE ANATOMY OF THE STEM AND SOME OTHER PARTS.

BY MIRIAM SHELDON.

Plates XVII to XXV.

INTRODUCTION.

SOME plant forms are peculiar and striking. Those of the desert are particularly individual, many being even grotesque in their chance variations. The choice of one of these plants for study was suggested by Professor Stevens, of the Botany Department of the University of Kansas. Accordingly, after sectioning and examining about fifty or sixty plants, I selected and studied three more carefully. Of these the subject of this sketch is perhaps the most interesting.

The material for this study was obtained in the summer of 1908. In July of that year collections of about sixty or seventy different species were made by Mr. L. M. Peace, of the University of Kansas laboratories. These were taken from the region around about Tucson, Ariz., representatives of some species being taken from several habitats, as from mesa, wash, irrigating ditch or hill top. As the short summer season of rains had just begun some of the plants were obtainable before the leaves had appeared. Specimens were, of course, also taken after the leaves came out. The jars with their preserving fluid (two per cent formalin) were taken into the field, and the plants put into these as soon as collected. In many instances the whole plant was secured, one jar containing the root, stem, leaves and flower or fruit of the same plant. It will be seen that this collection is particularly valuable because

of the great care taken in obtaining it. Many thanks are due Mr. Peace on this account, as well as for numerous verbal explanations and descriptions of the desert, the vegetation and the individual plants.

The literature dealing with the desert plants is, as is well known, somewhat meager. So far very little more than a description or a mere mention of *Koeberlinia* has been found. Gray describes it in his Plantæ Wrightianæ, and places it with the Rutaceæ. Engelmann mentions it twice in his works: once in his review of the Wislizenus plants and once as erroneously numbered by Emory among his Cactaceæ of the Southwest. Bentham and Hooker describe it under the family Simarubaceæ. The Ailanthus, or "Tree of Heaven," is perhaps the most familiar representative of this family with us northern dwellers among mesophytic forms. John Charles Van Dyke alludes to the "crucifixion thorn" in "The Desert." He says he has met with it in several localities although it is reported as "very scarce." Several travelers in Mexico and the Southwest have made collections of this plant or have reported it. Prof. Charles Bessey, of the University of Nebraska, in the "Burro Thorn" (*Holocantha emoryi*) finds a plant of great interest, if not one wholly as attractive morphologically, if one may judge by the brief account he was able to give for lack of the "oft promised material."

A description of the plant as a whole has not been found. We do not know that anyone has ever had the hardihood to dig up a root. It is said to make an impenetrable barrier, so that a plant three feet high is of such dense growth that the main stem is hardly to be seen. Among the earlier collectors of the plant might be mentioned Chas. Wright, Dr. Josiah Gregg, Gen. Wm. H. Emory and Dr. N. Wislizenus. The plant is sometimes called "Junco." It seems as the northern border of Mexico is approached the individual plants become more stunted and less numerous than farther south. The plant is thus described by Sargent:

"Leaves, not more than one inch long. Flowers, appearing in May and June, about one-fourth inch in diameter. A bushy tree, rarely twenty to twenty-five feet high, with a short, stout trunk sometimes six to eight feet long and a foot in diameter; more often a low-branching shrub forming impenetrable thickets, often of considerable extent. Wood very hard, heavy, close-grained, dark brown somewhat streaked with orange;

becomes almost black on exposure, with thin yellow or nearly white sapwood of twelve to fifteen layers of annual growth. Distribution: Dry gravelly mesas and foothills, valley of the Lower Rio Grande, Texas, westward to southern through northern Mexico."

The four or five plants seen by Mr. Peace were of various sizes, the largest—the one from which the specimens were taken—being about three feet wide and very compact in growth. The branches were pale green in color, no leaves, the flowers whitish to cream color. This was about three miles southwest of Tucson.

As far as observed every branch is a thorn, some of them a little blunt at the end and not tipped with the brownish needle-like point. The thorns vary from 1.5 cm. to 7 cm. in length, being from 1 mm. to 4 mm. in diameter at the base. The largest stem obtainable for study was about 4.5 mm. in diameter, and was probably five or six years old, possibly more. To all appearances the bark is smooth, but microscopically it is somewhat rough, the roughness due to the dome-shaped projections which occur over the stomatal chambers. The flowers are borne along the sides of very small sharp thorns. They have the appearance of being in a raceme—an umbel-like raceme, some authors call it. The leaves, said to be scalelike, are soon dropped.

INVESTIGATION.

The study of the desert plants was taken up in February, 1909, in connection with other graduate work at the University of Kansas, and continued until the middle of August of that year.

The methods employed in pursuance of this study were various. The chlor-zinc-iodide treatment of sections fresh from the formalin or paraffin, or softened from the dried state, proved on the whole the most satisfactory.

All the figures, except a few of the flower and some diagrammatic ones, were made by the aid of the camera lucida, the projection lantern or the photographic camera.

Stem.—The stem as a whole shows some interesting features in cross section, of which the thick epidermis, deeply sunken stomata, the deep palisade tissue, compact wood and small water tubes are not the least striking.

The *tissues* might be taken in their order, beginning with the innermost one. It has been observed that no generalization

can be made in regard to the structure of these desert plants, each one having its own peculiar way of getting on.

The *pith* occupies a sort of triangular area. The cells are comparatively large (see table), are heavily lignified, deeply pitted, stored with starchy material, and possessed of—in almost every case—a small crystal having the form of the calcium oxalate crystal. In the younger flower branch we find cells with thick walls, also, but retaining their rounded shape, pitted, and plentifully surrounded with air spaces. No food material was observed stored in this region. In the older stem elongated pit cells next the trachial tubes are densely filled with material that stains blue with c. z. i. This has a fine granular appearance (fig. 2, plate XX).

The *medullary rays* are conspicuously broad in cross section, many being five cells wide. The cells are comparatively large. They have the ordinary cylindrical shape with thick lignified and pitted walls. (Figs. 3 and 5, plate XIX.) Intercellular spaces are frequent. Most of the cells are full of non-nitrogenous material, while a few narrow and elongated ones appear adapted for quick conduction. Those between the phloëm strands show the characteristic proteid reaction with c. z. i. and have the usual unpitted walls. Crystals are often found in these cells.

The *xylem* makes up a great part of the stem. The wood fibers cannot be said to be very numerous. They have the usual shape and are rather short. (See table.) The fiber-tracheids are found quite plentifully and correspond closely to the wood fiber. The bordered pits, however, are very numerous, there being at least 200 to a tracheid. (Fig. 15, plate XX.) The pits are small. The spiral tracheids have the single and double spiral threads. These vessels are decidedly small. The tracheids are of three kinds and vary in length and diameter. (See table of measurements.) The tracheal tubes have many small bordered pits and have thickenings in ridges in the walls. The whole tube is divided at more or less regular intervals, as from 0.6 to 0.27 mm., by thick rings. Upon investigation these may sometimes be seen to be in the plane of union of neighboring tubes, the walls being so completely fused as to obliterate all trace of joining. It seems that these rings are really the borders of an aperture in the ends of tube elements, occurring in the earliest laying down of the tissue. They were observed in the last vessels laid down before col-

lecting in the midst of the rainy season of 1908. (See figs. 5 and 6, plate XX.) These pitted vessels, often with ragged inner thickenings (fig. 6), are found from the spiral vessels next the pith to the latest growth. They are also found in the young thorn which bears the flowers. The end of this division of the tracheal tube is often very much elongated and gradually tapering (figs. 3, 4, 9). Sometimes the long tapering is omitted and we have a peculiar cell ending as in figures 6*a* and 7. These elements sometimes taper at both ends, but frequently and abruptly in horizontal base. (Fig. 3.)

Besides the tube elements just described, there are the more or less rectangular tracheids that join their neighbors above or below by horizontal or oblique walls. (Fig. 13.)

No means to be had will give an exact account of the age of the stem. This is true of most of the perennials of the desert, we believe. Upon projecting upon the screen by means of the lantern, a cross section of the older stem showed traces of five or six seasons' growth, a slight increase in the size and number of the vessels being noticeable in each successive yearly growth as well as a somewhat greater compactness of growth in the wood itself. Probably for the year 1907 a new set of vessels has been formed. (Fig. 1, plate XVIII.) Outside of these is a second set of larger and unquestionably new water vessels laid down at the beginning of the rainy season of 1908. The width of an annual ring varies somewhat, but on the whole has an average of about 0.2 mm. The entire radial measurement of the wood from pith to phloëm is about 1.5 mm. This would make the stem about seven and a half years old.

The *Phloëm* region shows the usual storage of nitrogenous materials in the sieve and companion cell portion and in the parenchyma. The elements of the sieve vessels are rather long (see table) and full of fine granular material. The sieve plates are heavy, with very minute perforations on the sides. The phloëm parenchyma in my material occurs in a series of five parts, each being about three cells wide. (Fig. 1, plate XXI.)

The *stone cells* and *bast* make a hard, rigid cylinder around this more delicate portion, the stone cells occurring between the bundles of bast and extending around them.

The sclerenchymatous or stone cells are of various shapes: some are squarish, some oblong, and some so elongated as to be confused with the bast as far as shape goes, but possessing the deeply pitted characteristic of the stone cell. This zone

occupied by the stone cells is broad. Sometimes the cells are found in the region of the palisade cells, in scattered patches, or in many cases filling up air cavities below the stomatal chamber. (Fig. 1, plate XXIII.)

The bast appears to be of twofold character—the ordinary long, tapering cells, united by a long splicing, then another kind, shorter and tapering abruptly at one end, while the other end, rather blunt, fits securely into the socket made by the two cells below. (Figs. 8, 9, 10, plate XXI.) These fibers occur in the regular bundles, but they also make a sort of inner bundle, we think; at least, in all the cases so far examined they appear to occupy that position. They may make a sort of inner supporting shaft to the whole group. When separated from the long fibers a bundle of them looks like a barbed shaft.

The *spongy parenchyma* tissue takes up the inner collenchyma region. These are about five or six cells deep radially. The walls of some of the parenchyma of the innermost portion are heavily lignified. Neighboring cells have not so changed materially, but the cellulose wall is thicker in many cases. The walls in all the sponge are about twice as thick as those of the palisade region. The spongy cells are spherical, cuboidal or ovoid in shape, and about twice the diameter of the palisade cells. The numerous and large intercellular spaces in this region are conspicuous. There are besides whole rows of open spaces, seen in either cross- or longi-sections. (Fig. 9, plate XXII.) This will be taken up in a later paragraph, however.

The *palisade cells* lie in characteristic position, two or three deep radially. They are thin walled, cylindrical in shape, with some, but rather small, intercellular spaces. The chloroplasts are of goodly size, and show a deep blue in treating with c. z. i. In this region also are to be found very large aerating chambers, ovoid in shape, connecting directly with the stomatal chamber above, and thence with the outer world. These are not quite so numerous as the smaller cavities mentioned in the sponge. (Figs. 3, 4, plate XXII.)

The *epidermis* is remarkable. The cuticle itself is very heavy, it being 0.015 mm. in thickness in the old stem. The whole epidermis as found in the older stem measures from 0.075 mm. to 0.105 mm. There is but one row of epidermis cells. These are elongated radially, and in the younger parts of the plant are of thin cellulose walls. In the older parts the walls become very much thickened, so much so that in time only

a conical space at the bottom represents the cell cavity. (Figs. 4, 5, plate XXII.) At intervals these picket-like cells give way to large cavities, which they surround and protect by a slight modification at the outer extremity, a curving upward and inward, thus making a little dome of from eight to a dozen cell tips. (Figs. 3, 1, plate XXIII.) These, not entirely closing the cavity, leave an aperture allowing of communication between the outer world and the stomatal apparatus within and thence farther beyond to inner tissues. (Fig. 8, plate XXII.) The details of this arrangement, although seemingly complex, are actually simple. The stoma lies at the base of the epidermal air chamber; slight projections of the walls of the guard cells make a shallow stomatal chamber immediately above, and like ones make one below. Beyond the lower lies the large ovoid cavity referred to in the palisade tissue. (Figs. 8, 9, plate XXII, fig. 11, plate XXIII; and for measurements, see table, p. 7.) A curious little Phycomycete makes its home in the outside stomatal cavities. It occurs in a majority of the stem stomata. (Fig. 7, plate XXII.) There are about 150 stomata to a square millimeter. (Fig. 2, plate XXIII.) In the younger stem a tissue for water storage occurs just outside the pericycle. Sometimes this appears to be represented by a single cell only. (Figs. 8, 9, 10, plate XXIII.) The region of spongy parenchyma here stains deep blue with c. z. i., while the palisade cells remain yellowish.

Flower.—The flower, cream color to yellow, shows the four-parted arrangement—four very short triangular sepals, greenish in color; four long, blunt, prominently veined petals, enclosing eight stamens, which show an inequality in length of filament. The anthers are elongate-ovoid, and open on the side. They are attached to the filament at about one-fourth the distance from the base. The filaments are stout and tapering upward. The superior ovary is globose in shape, tapering above into a pillarlike style, which in turn tapers slightly at the apex to form the stigma, which is a plain surface surrounding a circular orifice.

Upon sectioning the ovary longitudinally the numerous ovules are noticed in longi-section; they appear hanging down from the central placenta. In cross section two cells are seen, and in some parts a suggestion of two side partitions. The ovary wall is cutinized heavily without and within, insuring

protection for the ovules against the intense aridity of the desert atmosphere. The mesophyll of the ovary is well supplied with chorophyll bodies and contains numerous mucilage cells, thus assisting in the provision for intensest drought. A resinous gum is found in the seed vessel surrounding the ovules and the vascular bundles in the placenta. (Figs. 1, 2, 3, 4, plate XXIV.) The resinous gum is not found elsewhere.

The contents of the cells of the stomata of the inner wall of the seed vessel stain a deep blue with c. z. i., showing that the guard cells here are living and filled with non-nitrogenous material.

The mucilage cells finally break down, thus forming large mucilage reservoirs. (Figs. 8, 7, 5, plate XXIV.)

CONCLUSION.

Koeberlinia is what Clements would call a stem xerophyte. The low stature of the plant, its compact habit of growth and the heavily cutinized surface everywhere, reduces evaporation to a minimum. The dead-air spaces furnished by the outer stomatal chambers also contribute toward this end. A supply of moisture is insured for the more strongly growing parts by the storage of water in special reservoirs and by the presence of mucilage in the seed vessel. The resinous gum aids in conserving moisture. Greater strength is secured, perhaps, through the peculiar splicing of the large tracheids. The stone cells, with their firm adherence to the bast fibers, also give strength. The air spaces in epidermis, palisade tissue, sponge, medullary rays and pith insure a goodly supply of CO_2 without much evaporation. These points might be summed up thus:

Evaporation minimized by:

1. Dispensing with leaves.
2. Heavy cutinization on all exposed surfaces.
3. Dead-air spaces (outer stomatal chambers).
4. Low stature.
5. Compact growth.
6. Resinous gum surrounding tender growths.

Moisture supply provided for by:

1. Special reservoirs for water storage.
2. Mucilage in cells in seed vessel.
3. Tracheal elements.
4. Presence of resinous gum.

Strength attained by:

1. Extreme lignification.
2. Long splicing of bast.
3. Long splicing of large tracheids.
4. Heavy zone of stone cells firmly adhering to bast.

Supply of air provided for by intercellular spaces in:

Epidermis.
Palisade.
Sponge.
Medullary ray.
Pith.

On the whole, this plant presents a wonderful array of "aids" to getting on in the desert. No other plant examined showed so thick an epidermis and such an aerating system. A few were almost leafless, a few had a heavy epidermis, some were strongly lignified, others showed resinous secretions. Almost all had larger water-conducting vessels. With all the adaptations that this plant had it seemed strange that it was so rare, but upon investigation we find that by abortion the many seeds are reduced to one, two or three to a berry. We have not yet found out whether the berry is eaten by animals or not.

Tables of measurement, rainfall and evaporation are presented for reference; also, a very superficial table giving some facts in regard to a few other desert plants. I am indebted to Mr. Peace for the tables on rainfall and evaporation. He has also kindly furnished the two photographs as well as much valuable information. Thanks are due to Doctor Trelease, Doctor Land and Doctor Spalding, for kindness in answering inquiries. I also wish to thank Doctor Billings for suggestions, and Professor Stevens especially for ever-ready assistance. It is a pleasure here to express gratitude to Doctor MacDougal for freely granting the facilities of the desert laboratory while the materials were being collected.

TABLE OF MEASUREMENTS.

	Structure.	*Length, mm.*		*Width, mm.*	
1.	Mid pith cell	0.03 to	0.045	0.03 to	0.075
2.	Marginal pith cell	.045	.075	.01	.015
3.	Medullary ray cell	.05	.075	.012	.014
4.	Wood fiber	.....	.24	.....	.....
5.	Fiber tracheid	.....	.25	.....	.015
6.	Tracheal tubes	.06	.27	.01	.03
7.	Tracheids	.....	.114	.015	.025
8.	Sieve cell	.03	.25	.....	.015
9.	Phloem parenchyma	.022	.12	.....	.015
10.	Stone cell	.05	.12	.015	.06
11.	Bast (long)	.06	.15	.....	.013
12.	Bast (short)	.015	.03	.....	.007
13.	Spongy parenchyma	.015	.03	.....	.02
14.	Palisade cells	.....	.....	.01	.012
15.	Epidermis, older stem	.....	.....	.075	.105
16.	Cutinized portion epidermis, old stem	.....	.....	.....	.075
17.	Epidermis flower branch	.....	.....	.....	.06
18.	Cutinized portion epidermis, flower stem	.....	.....	.....	.013
19.	Epidermis-ovary, outer	.....	.....	.03	.065
20.	Cutinized portion epidermis-ovary, outer	.....	.....	.01	.015
21.	Epidermis-ovary, inner	.....	.....	.02	.045
22.	Cutinized portion epidermis-ovary, inner	.....	.....	.....	.01
23.	Epidermis of anther	.....	.....	.....	.02
24.	Cutinized portion epidermis, antner	.....	.....	.....	.0019
25.	Epidermis of petal, outer	.....	.....	.....	.02
26.	Cutinized portion epidermis-petal, outer	.....	.....	.....	.0019
27.	Epidermis petal, inner	.....	.....	.....	.015
28.	Cutinized portion epidermis-petal, inner	.....	.....	.....	.0019
29.	Upper stomatal space	.....	.12	.....	.04
30.	Lower stomatal space	.....	.06	.....	.03
31.	Outer stomatal aperture	.....	.....	.....	.008
32.	Inner stomatal aperture	.....	.....	.....	.015
33.	Air space in sponge	.03	.045	.025	.032
34.	Mucilage cells	.....	.....	.....	.0325
35.	Mucilage reservoirs	.....	.....	.06	.15
36.	Water storage cells	.03	.06	.03	.045
37.	Resinous gum cells	.03	.092	.015	.02
38.	Intercellular space, pith	.....	.....	.007	.015
39.	Intercellular space, sponge	.....	.....	.003	.015

RAINFALL NEAR TUCSON.

Jan. 3	0.62 inch.	Apr. 23	0.11 inch.
" 15	.05 "	May 3	.05 "
" 23	trace.	" 23	.03 "
" 30	"	July 5	trace.
Feb. 3	0.29 inch.	" 7	0.04 inch.
" 4	.57 "	" 10	trace.
" 7	trace.	" 13	"
" 10	0.16 inch.	" 15	0.80 inch.
" 11	.47* "	" 16	1.00 "
" 13	.24† "	" 17	2.6 "
" 22	.15 "	" 19	.01 "
Mar. 4		" 23	.61 "
" 19	trace.	" 25	1.81 "
" 20	0.38 inch.	" 27	.02 "
" 26	.03 "	" 28	.42 "
" 27	.01 "	Aug. 2	.42 "

* With snow. † With sleet and snow.

TEMPERATURE AT THE DESERT LABORATORY.

	Lowest.	*Highest.*		*Lowest.*	*Highest.*
July 6	77° F.	99° F.	July 18	65° F.	74° F.
" 7	77	103	" 19	68	87
" 8	74	99	" 20	75	95
" 9	78	90	" 21	75	99
" 10	78	95	" 22	75	94
" 11	74	101	" 23	62	92
" 13	71	100	" 24	65	90
" 15	67	97	" 25	72	91
" 16	69	88	" 26	62	92
" 17	64	82	" 27	69	84

RAINFALL OF TUCSON VICINITY.

	1904.	1905.	1906.	1907.	1908.
January	....	1.91	0.60	2.47	0.67
February	....	4.11	1.26	0.08	1.89
March	....	4.27	0.31	0.41	0.52
April	....	3.11	0.34	0.00	0.11
May	1.29?	0.03	0.02	0.45	0.08
June	0.04	0.24	0.00	0.00	0.00
July	2.07	1.47	2.07	4.67	5.73
August	3.00	0.47	1.16	3.66	*0.42
September	0.61	2.24	0.28	0.28	....
October	0.07	0.05	0.01	0.95	....
November	0.05	4.52	0.66	0.74	....
December	1.07	0.90	4.40	0.00	....
Totals	8.20	23.31	11.10	13.72	9.42

* To August 2.

From July 5 to July 31 there were twelve days upon which rain fell. There was rain during one day of each of the months of April, May and June. (These statements apply only to the year 1908.)

WEEKLY AVERAGES OF EVAPORATION,

In cubic centimeters, from free surfaces at a height of 25 centimeters above the ground.

	June.	July.	August.	September.
Tuscon	338	228	212	278
St. Louis	112	157	140	137
Lincoln	96	90	113	144
Chicago	93	95	109	95
New York	...	48	63	35

Temperatures, July 5, 1908, to August 2, 1908: Lowest, 62° F.; highest, 103° F.

NAME.	Epi.	Pith.	Water tubes mm. × sec.	Wood.	An. ring.	Med. ray.	Bast.	Air space.	Storage.	
									Food.	Water.
Cassia covesii.....	Thin.	0.0015	0.03 even scat.	Dense.	'08 only.	1 cell wide.	Bundle.	In pith.	Rays.	
Celtis reticulata.....		0.007	0.045	Dense in patches.	0.45 mm. '07; prominent.	?	Narrow ring.		Pith.	
Cercidium torreyana.....		0.003	0.037	Dense mod.	0.07 mm. few; '06.	1 cell wide.	Bundle.		Pith.	Epedemics.
Covillia tridentata.....		0.006	0.05 to 0.015	Dense.	Slightly marked.		Heavy band.		Rays tracheids and pith.	Epidermis.
Encelia farinosa.....		0.0015	0.045	Trach. 0.001	0.27 mm.; plain.		Bundle.		Few pith.	
Fouquieria splendens....	Cells many.	0.0015	0.04	Fibers.				Frequent pith.		?
Jatropha.....		0.0015	0.06	Trach. only 0.05	0.6	1 cell wide.		In pith.	Rays—pith.	?
Koeberlinia spinosa.....	0.09 mm.	0.007	0.004 to 0.015	Dense fib.—trach.	0.21 mm. '07; prom.	2 to 5 cells wide.	Bundle.	Bark.	Rays—pith.	
Krameria.....	0.029	0.0025	0.03	Dense fib.—trach.	0.38, '07—0.6	1 cell wide.		Minute.	Pith.	
Phoradendron.....	0.022	0.003	0.03 to 0.015			Immense.			Everywhere.	
Parkinsonia microphylla,	0.007		0.06 to 0.09	Trach. 0.014	0.45 mm.; 9 yrs.	1-3 cells wide.			Pith.	
Prosopis velutina.....		0.005	0.07 to 0.015	Heavy in patches.	0.3 (?)	1 cell wide.			Tracheids.	
Sambucus.....	Sev. celled.	0.0015	0.037	Few fib. trach.	'07—0.37 mm.	1-3 broad.	Bundles.	Few large.	Trach. rays.	
Schinus mollis.....			0.03	Trachs. mostly.		Row large.	Little.	Few large.	Rays.	Bark.
Negundo sp.....		0.0015	0.045 to 0.015	Tracheids.	0.3 to 0.15 mm.	1 cell wide.	In bundles.		Rays and pith margins.	

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